



Resource allocation in angiosperms

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ABSTRACT

The 'principle of allocation' advocates that every organism partitions the resources available to it for meeting the requirements for growth, maintenance, defense and reproduction. The pattern and magnitude of allocation for various functions determine their relative importance during the lifespan of an organism. Together these patterns are expected to reflect resource economies in plant reproduction and have important implications in their life history strategies and evolution. The present communication brings into focus some of the studies done in this direction.

Keywords : allocation, economy, resource, reproductive effort.

The concept of energy allocation mentioned first by Cody (1966) to explain the significance of clutch size in birds was later applied to plants as well. The resources available to a living plant are always finite. Every organism partitions these resources to meet its requirements for growth, maintenance, defence and reproduction. This is what underlies the 'principle of allocation'. The pattern and magnitude of allocation for various functions determine their relative importance to the organism's life cycle (McArthur & Wilson 1967). This postulate has led to a spate of experimental studies on resource allocation. Most of these are devoted to the estimation of resources allocated to reproduction, which is expressed as Reproductive Effort (RE). Among those who have estimated reproductive effort in different flowering plant species, the prominent ones are, Harper (1967), Harper and Ogden (1970), Pitelka (1977), Hawthorn and Cavers (1978), Primack (1979) Thompson and Stewart (1981), Bierzychudek (1981), Schoen (1982), Cruden and Lyon (1985), Bazzaz and Reekie (1985), Goldman and Willson (1986), Samson and Werk (1986), Dunn and Sharitz (1991), Niklas (1993), Delph *et al.* (1993), Ashman (1994), Sharma and Koul (1995), Parker *et al.* (1995), Brunet and Charlesworth (1995), Ågren and Schemske (1995), Worley and Harder (1996), Sardras *et al.* (1997), Sharma *et al.* (1999), Kaul *et al.* (2002), Kumar and Kaul (2010), Kour *et al.* (2010) and Sharma *et al.* (2015).

As plants bearing hermaphrodite flowers represent the most common type in flowering plants (Yampolsky and Yampolsky 1922), most of the studies carried out on resource allocation concern these. However, attention to species having other sex expressions has also gained momentum over the years. The various works executed from time to time have led to the formulation of a variety of models. Most of these are the same as were initially developed for animal systems.

All models advocate:

i. A 1:1 allocation ratio to male and female functions in all outcrossing hermaphrodite plants (Charnov *et al.* 1976, Maynard Smith 1971 a, b, 1978, Charnov 1979 a, Ross and Gregorius 1983, Smith 1981).

- ii. Breakdown of 1:1 ratio of allocation following some amount of selfing (Charnov 1982, Charlesworth and Charlesworth 1981, 1987).
- iii. Lower average allocation to male function in animal- than in wind-pollinated taxa (Charlesworth and Charlesworth 1981, Charnov 1979b, Lloyd 1984).

A factor that underlies above predictions is the difference in fitness gain via male or female sexual role. A shift towards either sex is favoured by natural selection only if it increases parental fitness for each unit of energy or resource spent (Lloyd 1983, Goldman and Willson 1986).

Assumptions underlying resource allocation models-

- I. Most models are based on the assumption that reproduction is limited by the availability of resources. Biomass partitioning is, in a way, a reflection of the allocation of limiting resources because different functions may be limited by the same resource type (Bazzaz *et al.* 1987). Most of the studies undertaken so far indicate that at least female reproductive effort and reproductive success are often resource limited (Willson and Burley 1983). That is why large plant size and/or favourable nutrient status promote female investment, which is necessary to sustain the future sporophyte (Lloyd and Bawa 1984). Fitness of female reproductive success is limited in some cases, not by resources but, by pollen and/or pollinator availability (Bierzychudek 1981, Willson and Burley 1983). That is why fruit production varies with pollen availability. Rarely male reproductive effort is also limited by the availability of resources (Schemske 1978, also see Goldman and Willson 1986) and access to mates (Charnov 1982, Lloyd 1984).
- II. Models of sex allocation assume that the resources meant for reproduction must be equally shared between male and female functions. Therefore, increased allocation to one necessitates proportionate reduction on the other. In other words, under resource limiting conditions trade-offs may occur between allocation to male and female functions or among competing activities like growth, maintenance and

reproduction (Gadgil and Bossert 1970). Evidences in favour of both kinds of trade-offs are on record. Female plants of *Plantago lanceolata* set larger seeds and bear more inflorescences than hermaphrodite plants (Primack 1978) indicating that savings made from male sex track have been diverted to the female track. Same holds true for the other species of *Plantago* as well (Sharma 1990, Jamwal *et al.* 1998). A significant trade-off between male and female functions has also been observed in *Cucurbita foetidissima* (Kohn 1989). Support in favour of trade-off assumption is also provided by Ashman's (1994) studies on *Sidalcea oregano* ssp. *spicata*, Delph and Meagher's (1995) work on *Silene latifolia* and Delesalle and Mooreside's (1995) studies on *Lagenaria siceraria*.

III. It has been often claimed that reproductive effort is an invariable characteristic of a species or population (Hickman 1977, Primack 1978, Abrahamson 1979) and does not alter even when plants are subjected to various kinds of stress (Harper and Ogden 1970, Van Andel and Vera 1977). However, rapidly increasing number of studies report a high level of phenotypic variability in gender within populations of morphologically hermaphrodite plants (Primack and Lloyd 1980, Broyles and Wyatt 1997). This variability in sex expression is likely to get reflected in resource allocation pattern. Many studies clearly indicate that reproductive effort is a dynamic component of an annual species' adaptive strategy under water stress in desert environments/ecosystems. For instance, in *Erucaria hispanica* and *Brachypodium distachyon*, inter population differences in reproductive effort were greater under water stress, the main limiting factor for plant growth in a desert. These results indicate that variability in reproductive effort in response to drought is a critical and dynamic component of life history strategies in annual species in heterogeneous, unpredictable xeric environments (Aronson *et al.* 1993). The RE in populations of *Murdannia keisak* inhabiting undisturbed sites is greater than at the two thermally disturbed sites (Dunn and Sharitz 1991) suggesting plasticity in the response of plants to environment. These, and many more studies support Levins' (1963) and Jain's (1979) view that variability in resource allocation patterns holds adaptive significance in plants, particularly in those inhabiting fluctuating, unpredictable environments. Recently, Kumar and Kaul (2010) found that plants of disturbed and undisturbed populations of *Murdannia nudiflora* (L.) Brenan did not vary significantly in the magnitude of their RE. Despite the phenotypic plasticity in various vegetative characters it does not get reflected in the pattern of RE.

Estimation of resource allocation—Estimation of resources allocated to sexual reproduction in plants has been a subject of great debate (Goldman and Willson 1986),

particularly with regard to the parameter (e.g., biomass, carbon, nutrients, energy) to be utilised for measurement and that would reflect the true cost of individual floral structures (Harper 1977, Thompson and Stewart 1981, Reekie and Bazzaz 1987 a, b).

In the opinion of Goldman and Willson (1986) gross biomass of different organ types of a plant may not be a legitimate measure of the reproductive effort, since reproductive organs of many species are capable of photosynthesis, whereby they meet their energy requirements (Bazzaz *et al.* 1979). For instance, in *Ambrosia trifida*, photosynthesis by reproductive structures meets 41 and 51% carbon requirement of male and female inflorescences respectively (Bazzaz and Carlson 1979). Different workers have used different units to estimate resource allocation to reproduction. These include, dry weight, N content, ash and P contents, etc. They have observed significant differences between the results of different procedures (Lovett-Doust and Harper 1980).

Measures employed for quantifying reproductive effort

- (i) Crude estimates: Crude estimates involve leaf count and area, flower and floral organ number, pollen and ovule counts, seed output and weight (Bradbury and Hofstra 1976, Primack 1979, Gross and Soule 1981, Sharma and Koul 1995, Sharma *et al.* 1999) and harvest index (seed dry matter/total shoot dry matter; Sadras *et al.* 1997).
- (ii) Dry biomass method: In this widely employed method, different plant parts, namely root, stem, leaves, flowers, buds, fruits and seeds are oven-dried at 55-95°C for 24-72 hours. The parts so dried are weighed, and relative energy allocation estimated (Lovett-Doust and Cavers 1982, Cruden and Lyon 1985, Cumaraswamy and Bawa 1989, Dunn and Sharitz 1991, Campbell 1992, Reekie and Bazzaz 1992, Fox 1992, Niklas 1993, Delph *et al.* 1993, Aronson *et al.* 1993, Korpelainen 1994, Delesalle and Mooreside 1995, Sharma and Koul 1995, Worley and Harder 1996, Sadras *et al.* 1997, Kaul *et al.* 2002, Kour *et al.* 2010, Kumar and Kaul 2010). This method is simple and reproducible and therefore considered reliable.
- (iii) Oxygen bomb calorimetry method: The foliar and floral parts are burned in oxygen rich atmosphere, to release carbon dioxide, water and minerals. The energy so released is measured in terms of rise in the temperature of calorimeter. The change in temperature is proportional to the energy bound in that plant part. Despite a few limitations, this method is considered reliable index of resource allocation (Ogden 1974, Bradbury and Hofstra 1976, Smith and Evenson 1978, Schemske 1978).
- (iv) Estimation of elemental composition: Specific chemical components in different parts of a plant are determined which reflect the resources consumed in the differentiation of that particular part. The chemical constituents considered important for the purpose include

N, P and Glucose equivalents (Wallace and Rundel 1979); N, P, K, Mg, Ca (Mckone 1987); C, H, N (Dunn and Sharitz 1991); C (Chapman *et al.* 1992); N, P, K (Ashman 1994); starch, soluble carbohydrates, N, P, K, Ca, Mg, Na, Zn, Fe, Mn, Cu (Ruiters and Mckenzie 1994) and N, total phenolic content, K, P, Ca, Mg, Mn, B, Cu, Fe, Al & Zn (Cipollini and Whigham 1994).

- (v) Latest addition to the estimates mentioned above is atomic absorption spectroscopy (Guleryuz *et al.* 2006, Khan *et al.* 2011, Kaul and Saroop 2015).

Factors influencing resource allocation-Abrahamson (1979) listed the factors which influence resource allocation patterns in flowering plants. These include, seasonal fluctuations, habitat differences, mode of pollination, microclimate of the individual, herbivory and seed predation.

Many workers have proposed that annual species allocate more resources for reproduction than do their perennial counterparts (Pitelka 1977, Primack 1979, Abrahamson 1979, Primack and Antonovics 1982, Sharma and Koul 1995) perhaps because they allocate a sizeable share of the resources to seed production which improves their colonizing ability (though along with wide dispersal). On the contrary, perennials allocate greater share of their resources towards vegetative structures, which ensures their survival for years at a fixed site (Pitelka 1977, Abrahamson 1979).

Reviewing all the work available up to 1982, Waite and Hutchings made certain generalizations. Some of these are (Waite and Hutchings 1982):

- (a) Polycarpic species allocate 0-20% energy to seed production.
- ((b) Herbaceous perennials invest 0-15% of their annual net assimilates to seed formation.
- (c) Allocation in wild annuals is 15-30%.
- (d) Cultivated grain crops exhibit 24-40% allotment to reproductive output.

Many works attribute variation in resource allocation to reproduction to, their breeding system and several other factors (Sharma *et al.* 1999, 2015, Kaul *et al.* 2002). In inbreeding species, the reproductive effort in general is higher than that in the outbreeding taxa (Sharma *et al.* 1999). Reproductive effort also differs with the position a flower occupies in an inflorescence. If flowers at the base of an inflorescence extract more reproductive resources than do more distant flowers (Lee 1988), variation in RE in such cases, will exist within different flowers of the inflorescence.

Resource partitioning in a cleistogamous species-*Commelina benghalensis* exhibits variability in both foliar and floral features; every plant bears three types of branches and four types of flowers. The branches are subterranean (positively geotropic), sub aerial (diageotropic) and aerial (negatively geotropic) while flowers are uni-or bisexual and

chasmio- or cleisto-gamous (Koul *et al.* 2001, Kaul *et al.* 2000, 2002, Kaul and Koul 2009). Plants allocate ca. 15% of their total resources to reproduction, the major part of which (68.9%) is devoted to the production of aerial branches and the remaining is distributed to two other branch types (8.9% to sub-aerial and 22.2% to subterranean). The proportion of RE allocated to various branch systems is correlated with the availability of resources at the time of their differentiation. Despite variations, most of the results are in line with Charnov's sex allocation theory (Kaul 1998, Kaul *et al.* 2002). It would, however, be quite interesting to see the pattern of allocation in relation to nutrient supplementation and under stress conditions.

Resource partitioning to reproduction starts in the life cycle of *C. benghalensis* when seedlings are only at 7-10 leaf stage. Under laboratory conditions these floral buds are formed even earlier. Such an early allocation of energy for reproduction 'concurrent with continued vegetative growth' takes place in many amphicarpic plants and has been termed 'pessimistic strategy' by Zeide (1978) and Cheplick and Quinn (1982). They advocate that, this strategy has its selective basis in the relative vigour, survival and reproductive efficiency of the two types of seedlings that arise from aerial and subterranean seeds. This pattern of allocation is comparable to at least 8 other amphicarpic annuals belonging to 5 phylogenetically unrelated families (see Cheplick and Quinn 1982). Production of subterranean fruits prior to even the development of aerial inflorescences has been observed in *Amphicarpum purshii* (McNamara and Quinn 1977, Cheplick and Quinn 1982), *Gymnarrhena micrantha* (Koller and Roth 1964, Zeide 1978), *Emex spinosa* (Weiss 1980) and *C. benghalensis* (Maheshwari and Maheshwari 1955, Kaul 1998, Kaul *et al.* 2002). The aerial floral buds differentiate much later, when the plants are at the 17-19 leaf stage, as a part of the 'optimistic strategy'.

Not many cases have, however, been worked out in this regard and, probably neither are all known and await discovery. Thus, it would be too pre-emptive to draw a generalized conclusion about all known underground flowering plants.

From what has been said above it emerges that resource allocation is still a fertile but under known area of research in the field of plant reproductive biology. Despite a number of comprehensive treatises published in recent years (see Geber *et al.* 1999, Reekie and Bazzaz 2005, Harder and Barrett, 2006) our understanding and knowledge of factors influencing reproduction and hence life history strategy of plants, their quantitative assessments, and of quantitative relationships between reproductive investments and other associated costs are scanty and far from complete. Therefore, lot needs to be done before these research outputs can be utilized for the improvement of crop plants.

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REFERENCES

- Abrahamson WG 1979. Patterns of resource allocation in wild flower populations of fields and woods. *Am. J. Bot.* **66**(1) 71-79.
- Ågren J and Schemske DW 1995. Sex allocation in the monoecious herb, *Begonia semiovata*. *Evol.* **49**(1) 121-130.
- Aronson J, Kigel J and Schmida A 1993. Reproductive allocation strategies in desert and Mediterranean populations of annual plants grown with and without water stress. *Oecologia* **93** 336-342.
- Ashman TL 1994. Reproductive allocation in hermaphrodite and female plants of *Sidalcea oregano* ssp. *spicata* (Malvaceae) using four currencies. *Am. J. Bot.* **81**(4) 433-438.
- Bazzaz FA and Carlson RW 1979. Photosynthetic contribution of flowers and seeds to reproductive effort of an annual colonizer. *New Phytol.* **82** 223-232.
- Bazzaz FA and Reekie EG 1985. The meaning and measurement of reproductive effort in plants. In *Studies in Plant Demography: A festschrift for John L. Harper*, White J (ed.), Pp. 373-387, Academic Press, London.
- Bazzaz FA, Carlson RW and Harper JL 1979. Contribution to reproductive effort by photosynthesis of flowers and fruits. *Nature* **279** 554-555.
- Bazzaz FA, Chiariello NR, Coley PD and Pitelka CF 1987. Allocating resources to reproduction and defense. *Bioscience* **37**(1) 58-67.
- Bierzychudek P 1981. Pollinator limitation of plant reproductive effort. *Am. Nat.* **117** 838-840.
- Bradbury IK and Hofstra G 1976. The partitioning of net energy resources in two populations of *Solidago canadensis* during a single developmental cycle in southern Ontario. *Can. J. Bot.* **54** 2449-2456.
- Broyles SB and Wyatt R 1997. The pollen donation hypothesis revisited: A response to Queller. *Am. Nat.* **149**(3) 595-599.
- Brunet J and Charlesworth D 1995. Floral sex allocation in sequentially blooming plants. *Evol.* **49**(1) 70-79.
- Campbell DR 1992. Variation in sex allocation and floral morphology in *Ipomopsis aggregata* (Polemoniaceae). *Am. J. Bot.* **79**(5) 516-521.
- Chapman DF, Robson MJ, Snaydon RW and Caradus JR 1992. The growth and carbon allocation patterns of white clover (*Trifolium repens* L.) in plants of contrasting branching structure. *Ann. Bot.* **69** 523-531.
- Charlesworth D and Charlesworth B 1981. Allocation of resources to male and female functions in hermaphroditic plants. *Biol. J. Linn. Soc.* **15** 57-74.
- Charlesworth D and Charlesworth B 1987. The effect of investment in attractive structures on allocation to male and female functions in plants. *Evol.* **41**(5) 948-968.
- Charnov EL 1979a. The genetical evolution of patterns of sexuality: Darwinian fitness. *Am. Nat.*, **113** 465-480.
- Charnov EL 1979b. Simultaneous hermaphroditism and sexual selection. *Proc. Natl. Acad. USA* **76** 2480-2484.
- Charnov EL 1982. *The theory of sex allocation*. Princeton University Press, Princeton, NJ.
- Charnov EL, Maynard Smith J & Bull J 1976. Why be an hermaphrodite? *Nature* **263** 125-126.
- Cheplick GP and Quinn JA 1982. *Amphicarpum purshii* and the 'pessimistic' strategy in amphicarpic annuals with subterranean fruit. *Oecologia* **52** 327:332.
- Cipollini ML and Whigham DF 1994. Sexual dimorphism and cost of reproduction in the dioecious shrub *Lindera benzoin* (Lauraceae). *Am. J. Bot.* **81**(1) 65-75.
- Cody M 1966. A general theory of clutch size. *Evol.* **20** 174-184.
- Cruden RW and Lyon DL 1985. Patterns of biomass allocation to male and female functions in plants with different mating systems. *Oecologia* **66** 299-306.
- Cumaraswamy A and Bawa KS 1989. Sex allocation and mating systems in pigeon pea, *Cajanus cajan* (Fabaceae). *Pl. Syst. Evol.* **168** 59-69.
- Delesalle VA and Mooreside PD 1995. Estimating the costs of allocation to male and female functions in a monoecious cucurbit, *Lagenaria siceraria*. *Oecologia* **107** 9-16.
- Delph LE and Meagher TR 1995. Sexual dimorphism masks Life history trade-offs in the dioecious plant *Silene latifolia*. *Ecology* **76**(3) 775-785.
- Delph LE, Lu Y and Jayne LD 1993. Patterns of resource allocation in a dioecious carex (Cyperaceae). *Am. J. Bot.* **80**(6) 607-615.
- Dunn CP and Sharitz RR 1991. Population structure, biomass allocation and phenotypic plasticity in *Murdannia keisak* (Commelinaceae). *Am. J. Bot.* **78**(12) 1712-1723.
- Fox JP 1992. Pollen limitation of reproductive effort in willows. *Oecologia* **90** 283-287.

- Gadgil M and Bossert WH 1970. Life historical consequences of natural selection. *Am. Nat.* **104** 1-24.
- Geber MA, Dawson TE and Delph LF (eds.) 1999. *Gender and sexual dimorphism in flowering plants*, Springer-Verlag, Berlin.
- Goldman DA and Wilson MF 1986. Sex allocation in functionally hermaphroditic plants: A review & critique. *Bot. Rev.* **52**(2) 157-194.
- Gross KL and Soule JD 1981. Differences in biomass allocation to reproductive and vegetative structures in male & female plants of a dioecious, perennial herb, *Silene alba* (Miller) Kraux. *Am. J. Bot.* **68** 801-807.
- Guleryuz G, Arslan H, Isgi B and Gucer S 2006. Element content (Cu, Fe, Mn, Ni, Pb& Zn) of the ruderal plant *Verbascum olympicum* Boiss. from East Mediterranean. *Zeitschrift für Naturforschung* **61** 357-362.
- Harder LD and Barrett SCH (eds.) 2006. *Ecology and evolution of flowers*, Oxford University Press, New York.
- Harper JL and Ogden J 1970. The reproductive strategy of higher plants. I. The concept of strategy with special references to *Senecio vulgaris* L. *J. Ecol.* **58** 681-698.
- Harper JL 1967. A Darwinian approach to plant ecology. *J. Ecol.* **53** 247-270.
- Harper JL 1977. *Population biology of plants*. Academic Press, New York.
- Hawthorn WR and Cavers PB 1978. Resource allocation in young plants of two perennial species of *Plantago*. *Can. J. Bot.* **56** 2533-2537.
- Hickman JC 1977. Energy allocation and niche differentiation in four co-existing annual species of *Polygonum* in western North America. *J. Ecol.* **65** 317-326
- Jain SK 1976. The evolution of inbreeding in plants. *Ann. Rev. Ecol. Syst.* **7** 469:495.
- Jamwal S, Dhar MK and Koul S 1998. Male sterility in *Plantago ovate* Forsk. *Curr. Sci.* **74** 504-505.
- Kaul V 1998. Resource allocation in relation to floral structure and breeding system in some members of family Commelinaceae. Ph. D. dissertation, University of Jammu, Jammu.
- Kaul V and Koul AK 2009. Sex expression and breeding strategy in *Commelina benghalensis* L. *J. Biosci.* **34** 977-990.
- Kaul V and Saroop S 2015. Techniques involved in reproductive biology-newer insights and future perspectives. In: *Plant Reproductive Biology and Conservation*, pp. 110-140. Kapoor R, Kaur I and Koul M (eds.). IK International Publishing House Pvt. Ltd., New Delhi.
- Kaul V, Koul AK and Sharma MC 2000. The Underground flower. *Curr. Sci.* **78**(1) 39-44.
- Kaul V, Sharma N and Koul AK 2002. Reproductive effort and sex allocation in *Commelina benghalensis* L., a common monsoon weed. *Bot. J. Linn. Soc.* **140** 403-413.
- Khan KY, Khan MA, Niamat R, Mamoona M, Fazal H, Mazari P, Seema N, Bashir T, Kanwal A and Ahmed SN 2011. Element content analysis of plants of genus *Ficus* using atomic absorption spectrometer. *Afri. J. Pharm. Pharmacol.* **5** 317-321.
- Kohn JR 1989. Sex ratio, seed production, biomass allocation, and the cost of male function in *Cucurbita foetidissima*. *Evol.* **43** 1424-1434.
- Koller D and Roth N 1964. Studies on the ecological and physiological significance of amphicarp in *Gymnarrhena micrantha* (Compositiae). *Am. J. Bot.* **51** (1) 26-35.
- Korpelainen H 1994. Sex ratios and resource allocation among sexually reproducing plants of *Rubus chamaemorus*. *Ann. Bot.* **74** 627-632.
- Koul AK, Kaul V and Sharma N 2001. Comparative reproductive efficiency of the above and underground flowers. In: *Botanical Essays: Tribute to Professor Bahadur Singh*, pp. 1-13. Chauhan SVS and Chaturvedi SN (eds.) Printwell Publ. Distrib., Jaipur.
- Kour H, Sharma I and Sharma N 2010. Sexual RE (SRE) and resource partitioning in three species of *Phyllanthus* L. *The Int. J. Pl. Reprod. Biol.* **2**(1) 99-103.
- Kumar R and Kaul V 2010. Reproductive effort in two populations of *Murdannia nudiflora* (L) Brenan. *The Int. J. Pl. Reprod. Biol.* **2**(2) 161-166.
- Lee TD 1988. Patterns of fruit and seed production. In: Lovett-Doust J & Lovett-Doust L (eds.) *Plant Reproductive Ecology: Patterns and Strategies*, Oxford University Press, New York. Pp. 179-202.
- Levins R 1963. Theory of fitness in a heterogeneous environment. II. Developmental flexibility and niche selection. *Am. Nat.* **97** 75-90.
- Lloyd DG 1983. Selection of combined versus separate sexes in seed plants. *Am. Nat.* **120** 571-585.
- Lloyd DG 1984. Gender allocations in outcrossing co-sexual plants. In: *Perspectives in plant population ecology*.

- Dirzo R and Sarukhan J (eds.), pp. 277-300, Sunderland Hars, Sinauer.
- Lloyd DG and Bawa KS 1984. Modification of the gender of seed plants in varying conditions. *Evol. Biol.* **17** 255-338.
- Lovett-Doust J and Cavers PB 1982. Biomass allocation in hermaphrodite flowers. *Can. J. Bot.* **60** 2530-2534.
- Lovett-Doust J and Harper JL 1980. The resource costs of gender and maternal support in an andromonecius umbellifer *Smyrniolobos olusatrum* L. *New Phytol.* **85** 251-264.
- Maheshwari P and Maheshwari JK 1955. Floral dimorphism in *Commelina forskalaei* Vahl. & *C. benghalensis* L. *Phytomorphology* **5** 413-422.
- Maynard-Smith J 1971a. What use is sex? *J. Theor. Biol.* **30** 319-335.
- Maynard-Smith J 1971b. The origin and maintenance of sex. In *Group Selection* (Williams Gc ed.) Aldind Atherton Inc., Chicago.
- Maynard-Smith J 1978. *The evolution of sex*. Cambridge University Press, Cambridge.
- McArthur RH and Wilson EO 1967. *Island biogeography*, Princeton University Press, Princeton, New Jersey.
- Mckone MI 1987. Sex allocation and outcrossing rate: A test of theoretical predictions using bromegrasses (*Bromus*). *Evol.* **41**(3) 591-598.
- McNamara J and Quinn JA 1977. Resource allocation and reproduction in populations of *Amphicarpum purshii* (Gramineae). *Am. J. Bot.* **64**(1) 17-23.
- Niklas KJ 1993. Allocation of organ biomass in perfect and imperfect flowers. *Ann. Bot.* **72** 475-483.
- Ogden J 1974. The reproductive strategy of higher plants. II. The reproductive strategy of *Tussilago furfura* L. *J. Ecol.* **62** 291-324.
- Parker IM, Nakamura RR and Schemske DW 1995. Reproductive allocation and the fitness consequences of selfing in two sympatric species of *Epilobium* (Onagraceae) with contrasting mating systems. *Am. J. Bot.* **82**(8) 1007-1016.
- Pitelka LF 1977. Energy allocation in annual and peremial lupines (*Lupinus*: Leguminosae). *Ecol.* **58** 178-194.
- Primack RB 1978. Regualtion of seed yield in *Plantago*. *J. Eco.* **66** 835-847.
- Primack RB 1979. Reproductive effort in annual and perennial species of *Plantago* (Plantaginaceae). *Am. Nat.* **114**(1) 51-62.
- Primack RB and Antonovics J 1982. Experimental ecological genetics in *Plantago* VIUI. Reproductive effort in populations of *P. Lanceolata* L. *Evol.* **36** 742-752.
- Primack RB and Lloyd DG 1980. Andromonoecy in the New Zealand montane shrub manuka, *Leptospermum scoparium* (Myrtaceae). *Am. J. Bot.* **67** (3) 361-368.
- Reekie EG and Bazzaz FA 1987a. Reproductive effort in plants. 1. Carbon allocation to reproduction. *Am. Nat.* **129** 876-896.
- Reekie EG and Bazzaz FA 1987b. Reproductive effort in plants. 2. Does carbon reflect the allocation of other resources? *Am. Nat.* **129** 897-906.
- Reekie EG and Bazzaz FA 1992. Cost of reproduction as reduced growth in genotypes of two congeneric species with contrasting life histories. *Oecologia* **90** 21-26.
- Reekie EG & Bazzaz FA (eds.) 2005. *Reproductive allocation in plants*. Elsevier Academic Press, London.
- Ross MD and Gregorius HR 1983. Outcrossing and sex function in hermaphrodites: a resource- allocation model. *Am. Nat.* **123** 204-222.
- Ruiters C and Mckenzie B 1994. Seasonal allocation and efficiency patterns of biomass and resources in perennial geophytes *Sparaxis grandiflora* sub sp. *fimbriata* (Iridaceae) in lowland coastal Fymbos, South Africa. *Ann. Bot.* **74** 633-646.
- Samson DA and Werk KS 1986. Size-dependent effects in the analysis of reproduction effort in plant. *Am. Nat.* **127** 667-680
- Sadras VO, Bange MP and Milroy SP 1997. Reproductive allocation of cotton in response to plant & environmental factors. *Ann. Bot.* **80** 75-81.
- Schemske DW 1978. Evolution of reproductive characteristics in *Impatiens* (Balsaminaceae) : The significance of cleistogamy & chasmogamy. *Ecol.* **59**(3) 596-613.
- Schoen DJ 1982. Male reproductive effort and breeding system in an hermaphroditic plant. *Oecologia* **53** 253-257.
- Sharma I, Sharma E and Sharma N 2015. Resource allocation in relation to meiotic system in two species of *Artemisia* abounding North-West Himalayas. *Caryologia* (In press).
- Sharma N and Koul AK 1995. Reproductive strategies in weeds—*Plantago major*; *P. lanceolata* and their cultivated ally *P. ovata*. *Proc. Indian Nat. Sci. Acad.* **B61** (6) 471-478.

- Sharma N, Koul AK & Kaul V 1999. Patterns of resource allocation of six *Plantago* species with different breeding systems. *J. Pl. Res.* **112** 1-5.
- Sharma N 1990. Genetic systems in *Plantago ovata* Forsk. and some of its allies. Ph.D. Thesis, University of Jammu.
- Smith CA and Evenson WE 1978. Energy distribution in reproductive structures in *Amaryllis*. *Am. J. Bot.* **65** 714-716.
- Smith CC 1981. The facultative adjustment of sex ratio in lodgepole pine. *Am. Nat.* **118** 297-305.
- Thompson K and Stewart AJA 1981. The measurement and meaning of reproductive effort in plants. *Am. Nat.* **117** 205-211.
- vanAndel J and Vera F 1977. Reproductive allocation in *Senecio sylvaticus* and *Chamenerion angustifolium* in relation to mineral nutrition. *J. Ecol.* **65** 747-758.
- Waite S and Hutchings MJ 1982. Plastic energy allocation pattern in *Plantago coronopus*. *Oikos* **38** 333-342.
- Wallace CS and Rundel PW 1979. Sexual dimorphism and resource allocation in male and female a hrubs of *Simondsia chinensis*. *Oecologia (Berl.)* **44** 34-39.
- Weiss PW 1980. Germination, reproduction and interference in the amphicarpic annual *Emex spinosa* (L.) Campd. *Oecologia (Berl.)* **45** 244-251.
- Willson MF & Burley N 1983. *Mate choice in plants*. Princeton University Press, Princeton, New Jersey.
- Worley AC and Harder LD 1996. Size-dependent resource allocation and costs of reproduction in *Pinguicula vulgaris* (Lentibulariaceae). *J. Ecol.* **84** 195-206.
- Yampolsky C and Yampolsky HY 1922. Distribution of sex forms in the phanerogamic flora. *Bibliotheca Genetica* **3** 1-62.
- Zeide B 1978. Reproductive behaviour of plants in time. *Am. Nat.* **112** s636-639.